

Phylogenetic Proximity and Nestedness in Mutualistic Ecosystems

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Abstract

We investigate how the pattern of contacts between species in mutualistic ecosystems is affected by the phylogenetic proximity between the species of each guild. We develop several theoretical tools to measure that effect and we use them to examine some real mutualistic systems. We aim at establishing the role of such proximity in the emergence of a nested pattern of contacts. We conclude that although phylogenetic proximity is compatible with nestedness it can not be claimed to determine it. We find that nestedness can instead be attributed to a general rule by which species tend to behave as generalists holding contacts with counterparts that already have a large number of contacts. A nested ecosystem generated by this rule, shows high phylogenetic diversity. This is to say, the counterparts of species having similar degrees are not phylogenetic neighbours.

Keywords: Nested networks; Mutualistic communities; Phylogenetic proximity; Extinction

1. Introduction

A sustainable management of ecosystems as well as a proper assessment of the impact of human activity on them can only be achieved with a proper understanding of the pattern of the interactions between the species. We are here interested in the case of mutualistic systems. These usually involve groups of animals and plants, helping each other to fulfill essential biological functions such as feeding or reproduction. This is the case of systems in which animals feed from fruits while dispersing the seeds (*seed dispersal networks*) or insects feed from the nectar of flowers while helping the plant in the pollination process (*pollination networks*).

The structure of such systems is described by means of an *adjacency matrix* whose elements rep-

resent the absence or presence of an interaction between the plant and animal species. This information when concerning mutualistic networks strongly indicates that they are not a random collection of interacting species, but they instead display a high degree of internal organization. A pervading feature that has been observed is that the adjacency matrix is nested, i.e. if species are ordered by increasing number of contacts, those of one species turn out to be nearly a proper subset of the contacts of the next species in the list [1]. This organization indicates that the *generalists* of both type of species (i.e. those species that interact with a great number of species of the other guild) tend to interact among them while there are no contacts among *specialists* (i.e. species that interact with very few species of the other guild).

The nested structure of mutualistic networks has been attributed to a number of different causes and there is still some degree of controversy about the ultimate reasons that make this pattern so fre-

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quently observed. It is fairly obvious that a detailed explanation of the interaction behavior of individual species can be of little help to understand such a generalized pattern that is found across ecological systems of very different sizes and types, and involving plants of different nature and animals that range from insects to birds.

In Ref.[2] it is claimed that such order may offer some advantage for the robustness of the whole system thus suggesting that systems that are currently observed are those that have survived less disturbed thanks to its nested structure. Other, more elaborated theories have been proposed. In Ref.[3] nestedness has been attributed to phenotypic affinity between species of different guilds while in Ref.[4] an extensive analysis is made concluding that phylogenetic proximity could explain the nested organization of contacts of some cases of mutualistic systems. A somehow different point of view about this work can be found in Ref.[5].

It has been customary to consider that the occurrence of some positive statistical correlation is a sign of causation for the occurrence of the nested pattern of contacts. However, the sole fact that in a part of the empirical observations two elements appear to be statistically correlated should not be taken to mean that one is the cause of the other. Such correlation may rather indicate instead that both elements are not incompatible, i.e. that they do not mutually exclude each other or that they stem from a third, common cause. One alternative way to search for causal relationships is to explore the possible dynamic consequences of some assumed interaction mechanism, thus validating or falsifying hypotheses concerning possible interaction mechanisms between the species. In Refs. [6], [7] we have proposed a dynamic model, the Self Organising Network Model (SNM), that allows to study the contact pattern of a system that is consistent with some hypothetical interaction mechanism between mutualistic species.

One example of this analysis is given by the strong positive correlation found between the species' abundance and hence the frequency of interactions, with the pattern of contacts of some species [8]. It has been suggested that locally abundant species are prone to accumulate interactions and conversely rare species are prone to lose them [9], as also suggested by neutral theories [10]. However, a dynamic analysis succeeds in generating a realistic distribution of species degree *under no assumptions* whatsoever on species abundance. A re-

verse interpretation may therefore appear also to be possible, i.e., that accumulation of interactions occurs first, and the resulting higher reproductive success leads later to local abundance. With such dynamic modeling and by comparison with the observed natural systems, it is possible to reject or retain some hypothetical interaction mechanisms as a possible cause of the observed order.

In considering real ecological systems one should perhaps expect that a single yet universal cause may be the prime responsible of inducing nestedness but that other minor causes may help to shape down the observed pattern of interactions of each individual case. This state of affairs indicates the convenience of finding one or more, model independent tests that can directly be performed on observational data to gauge the degree in which an observed pattern of contacts [11] is governed by some presumed cause.

In the present paper we develop several theoretical tools to measure the effect of phylogenetic proximity in the contact pattern of the system and use them to examine some real mutualistic systems. We aim in this way at establishing whether such proximity can be taken to be responsible for the emergence of a nested pattern of contacts, while some other minor causes may explain departures in particular circumstances.

2. Theoretical Background

Mutualistic systems can be analyzed as bipartite graphs [13]. The interaction pattern is usually coded into a (rectangular) adjacency matrix in which rows and columns are labeled respectively by the plant and animal species. Its elements $K_{p,a} \in \{0,1\}$ represent respectively the absence or presence of an interaction (contact) between the plant species p and the animal species a . The degrees of each plant or animal species can be obtained from this matrix as:

$$G^P(p) = \sum_a K_{p,a} K_{a,p}^T \quad (1)$$

$$G^A(a) = \sum_p K_{a,p}^T K_{p,a} \quad (2)$$

where $K_{a,p}^T$ is the trasposed of the adjacency matrix.

In order to explore the connection between the phylogenetic structure of plants and animals and

the corresponding pattern of contacts we will assume that a phylogenetic tree has been established for animals and plants. All species are therefore taken as the leafs or tips of a tree-like diagram that represents their evolutionary history.

A prevailing phylogenetic order can be represented as a matrix of phylogenetic distances between species. In the literature this is obtained from the expected covariance of traits between pairs of species through a comparison between real data sets and the results of a random walk along the tree topology. This way of measuring distances is based on the statistical model for the transmission of characters along the tree and is therefore model dependent. Instead of this we use a more direct, unambiguous and model independent way defining the phylogenetic distance extracting its value from the topology of the phylogenetic tree as the number of nodes that have to be explored following the tree and starting from either species, until a common ancestor of the two species is found. The phylogenetic distance $d(k, k')$ between any two species k, k' is then defined as the maximum number of nodes that are found starting from k or k' . With this definition the closest distance between any two species is 1. If all species are at a distance 1 then all species belong to a so-called *star-phylogeny*.

This definition is a simplified version of a more elaborate *ultrametric* [14] distance in which a meaning is ascribed to the length of the branches of the tree by relating it to the time involved in the evolutionary history. The distance that we have defined however satisfies all the requirements of a metric function and it also provides values that fully agree with an intuitive picture. A small value of $d(k, k')$ remains associated to species that share the same branching sequence in a common evolutionary history and a large value corresponds to species that have been separated at earlier stages.

To test for the effects of phylogenetic proximity in the pattern of contacts we will consider static and dynamic approaches. Among the former we will consider the effects of the ecological similarity between species, the robustness of the model and the direct correlation between the degrees of pairs of species and their phylogenetic distance. Among the later we will study the stability of some contact patterns when different rules governing the interaction between mutualistic counterparts are considered.

2.1. Static test I: Correlations with the phylogenetic distance

In order to study the influence of phylogenetic proximity we investigate the dependence of two parameters with the phylogenetic distance. One is the *ecological similarity* $S_{k,k'}$ and the other is the dispersion of the degrees $G(k)$ and $G(k')$ of pairs of species k, k' separated by a given phylogenetic distance.

The ecological similarity is defined [4] as

$$S_{k,k'} = \frac{W_{k,k'}^{A,(P)}}{G(k) + G(k')} \quad (3)$$

In (3) the matrix $W_{k,k'}^{A,(P)}$ corresponds to the *projected graphs* whose matrix elements measure the number of mutualistic counterparts that are shared by the species k and k' . The matrix W for plants or animals are obtained through $W^P = KK^T$ or $W^A = K^TK$. The parameter 3 measures the number of mutualistic counterparts shared by the two species as compared to the total number of counterparts of both, in this way, $S_{k,k'}|_{\max} = 1/2$. In order to consider the dependence with the distance we consider the average $\langle S(\delta) \rangle$ defined as

$$\langle S(\delta) \rangle = \frac{1}{N_\delta} \sum_{(k,k')|d(k,k')=\delta} S_{k,k'} \quad (4)$$

where N_δ is the number of pairs of species of the same guild that are separated by a phylogenetic distance δ .

If phylogenetically close species share some common feeding or polinization strategy, they should also be expected to have similar degrees Ref.[4]. The second parameter that we consider is therefore the dispersion of the degrees of pairs of species as a function of the phylogenetic distance. We define:

$$\Delta G^{A,(P)}(\delta) = \sqrt{\frac{1}{N_\delta} \sum_{(k,k')|d(k,k')=\delta} \left(G_k^{A,(P)} - G_{k'}^{A,(P)} \right)^2} \quad (5)$$

where G_k is the degree of the species k . The sum is extended over all pairs of species (k, k') that are separated by the phylogenetic distance δ .

2.2. Static test II: Robustness analysis

Given the adjacency matrix of a mutualistic system it is possible to get a measure of the robustness of the system. It has been customary [16] to

do this through an *attack tolerance curve* (ATC). The basic idea is that if an “attack” is made by which some fraction of the species of one guild is eliminated, a number of species of the other will become extinct because they are left without their mutualistic counterparts. It is of course also possible to determine the species that *survive* to the above attack.

In order to use this concept to study the effect of the phylogenetic structure of the species that belong to the mutualist system the ideas involved in the ATC have to be generalized. Instead of limiting the analysis to the *number* of species that survive or become extinct, one can rather study the *phylogenetic relation* between the surviving species, by keeping track of the average phylogenetic distance between them.

In order to do so we construct a Generalized ATC (GATC) in which nestedness and phylogeny are simultaneously considered. Nestedness is taken into consideration by orderly eliminating the species of one guild according to their degrees while the phylogenetic structure of the partially depleted counterpart guild is tested through the average phylogenetic distance between the surviving species.

2.3. Dynamic test: the SNM

Several arguments have been put forward to support that the pattern of interactions between the two guilds of a mutualistic network is due to some underlying reason. Most of those hypotheses lie upon statistically significant, observed correlations between some parameters. Correlation is however not the same as causation. One way out to elucidate a possible causal link between some hypothesis about the interaction mechanisms of the species and a given interaction pattern, is to explore eventual consequences of such hypothesis through a dynamic model.

The basic idea behind this modeling strategy is to verify the *consistency* of the empirically observed contact pattern, with some hypothetical interaction rule that may favor or hamper the contact between mutualist species. We refer to such interaction mechanism as a contact preference rule (CPR). An instability may easily be detected when the observed adjacency matrix tends to be drastically changed if species are allowed to redefine their contacts to make a better use of some assumed CPR. Within the same reasoning it is also possible to check the features of the contact pattern that *emerges* from an initial random adjacency matrix

if iterated changes of this type are allowed to take place. This can give a clue of what one should expect to observe in nature if some given CPR is the prevailing interaction mechanism among the species of system. This kind of analysis allows to trace possible causal relationships between a generalized individual behavior and the features of the global pattern of contacts.

From a purely theoretical point of view the above considerations are equivalent to consider that the observed pattern of interactions corresponds to an optimal assignment of the contacts between both guilds, with two constraints, first the fulfillment of some hypothetical, generalized, individual behavior trait and second, the total energy expenditure of all the species of the ecological system in their search for contacts. In other words one may attempt to describe the observed pattern of contacts as the result of a (combinatorial) *optimization* problem by which contacts in the adjacency matrix are placed in such a way as to reach an extreme of some utility function defined in terms of the prevailing CPR.

An example of a dynamic model of this kind is the SNM [2] [6]. This has been introduced in order to account for nestedness in mutualistic webs. Within that model, the mutualistic system is assimilated to a bipartite graph and the topology of the corresponding network is established as the result of a self-organization process. This amounts to progressively redefine the links obeying some hypothetical CPR that is assumed to prevail among the nodes of the network. In Refs.[2],[6] we show that a CPR where species tend to have contacts with counterparts that already hold a greater number of contacts leads to nested networks.

The fulfillment of the additional constraint of limiting the total energy consumed by all the species belonging to the system is built into the model by imposing that the self organization process takes place keeping constant the total number of contacts. It is therefore implicitly assumed that on the average, the establishment of each contact involves some fixed amount of energy. One could consider that this is spent in the process of searching for the counterpart.

It is worth to stress that the self-organization process *does not represent a real life behavior* of plants and animals of the system. It therefore does not aim at reproducing any evolutive or adaptive process. It rather provides a plausible mathematical tool to check for instabilities and to search for contact patterns that are optimal in the sense explained above.

3. Results: Tests of the effects of phylogenetic proximity

We now turn to provide a measure of the influence of the phylogenetic proximity by focusing our attention in a set of systems that have been reported in Ref. [4] (NCOR, OLAU, ARR1 and ARR2). Additionally, we take as a reference an idealized situation through a benchmark system of comparable size that we call PERF (36 plants and 50 animals). This is constructed in such a way that its adjacency matrix is perfectly nested and contacts faithfully follow some assumed (arbitrary) phylogenetic ordering. The phylogenetic tree and the adjacency matrix are tailored to perfectly match each other, in the sense proposed in [4]. The adjacency matrix together with the (arbitrary) phylogenetic trees are shown in Fig.1.

In all cases we also consider null models consisting of systems in which the adjacency matrix and the structure of phylogenetic trees of both guilds are the same as the observed ones but the species labeling the tips are randomly permuted. We refer to these as the "randomized" versions of either the real observed system or the ideal PERF-system. The null model is constructed considering the average over many realizations of such random sorting. This is done to provide statistically significant results of a situation in which the correlation between the structure of the network and the prevailing phylogenetic order has been destroyed.

3.1. Correlations with the phylogenetic distance

In Fig.2 where we plot the average ecological similarity $\langle S(\delta) \rangle$ defined in Eq.(4) as a function of the distance δ separating any pair of species of the NCOR and PERF systems.

It can be seen that for the PERF-system $\langle S(\delta) \rangle$ decreases monotonically with the phylogenetic distance for plants and animals. This monotonous trend is destroyed in the corresponding randomized system. In the same plots made for the NCOR-system there is no qualitative difference between the real and the randomized case.

In Fig.3 we show the plots of $\Delta G^{A(P)}(\delta)$ as defined in Eq.(5) for all the systems (NCOR, OLAU, ARR1, ARR2) together with the one corresponding to the PERF benchmark system. If the number of contacts were governed by the phylogenetic proximity, the smallest value of $\Delta G(\delta)$ should be found at

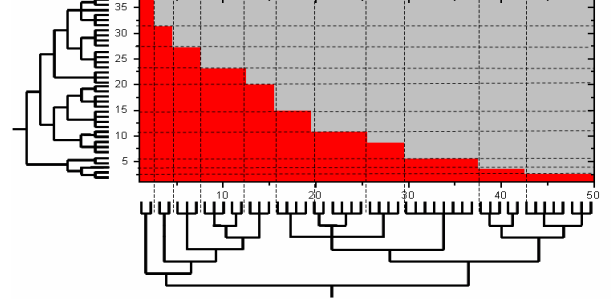


Figure 1: Adjacency matrix of the benchmark PERF system in which a perfectly nested contact pattern is tailored to follow the (arbitrary) phylogenetic tree of animals and plants. Dotted lines are drawn to help the eye in the correspondence of contacts with phylogenetic groups

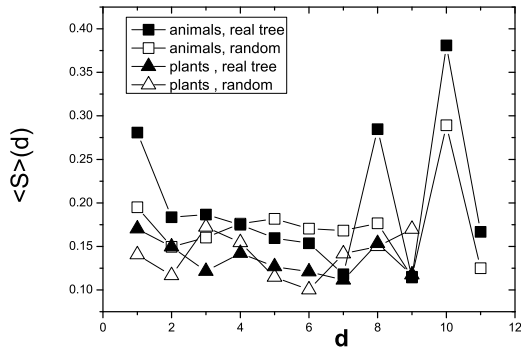
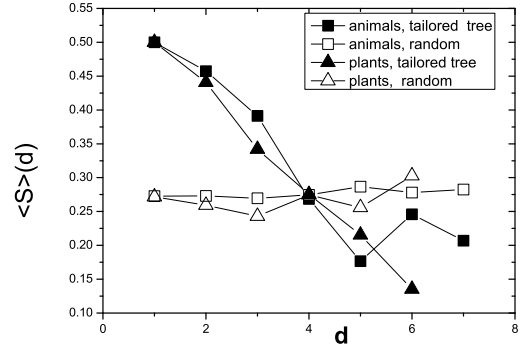


Figure 2: Average ecological similarity as a function of the phylogenetic distance for plants and animals. We show in the same graph the results corresponding to both, the ordered and the randomized phylogenetic tree. Upper panel: PERF-system. Bottom panel: NCOR matrix.

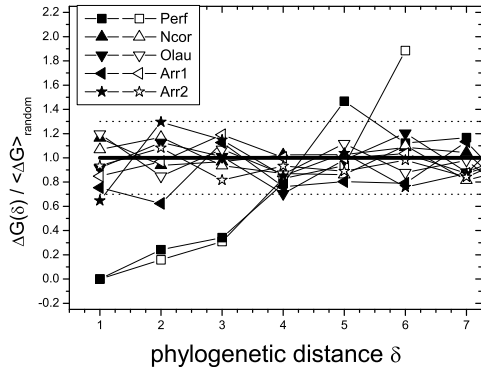


Figure 3: ΔG as a function of the phylogenetic distance δ for $\delta \leq 7$. Filled (empty) symbols represent animals (plants). In every case, the values are normalized by dividing them by the average obtained from the null models for the PERF, NCOR, OLAU, ARR1 and ARR2 systems $\langle \Delta G \rangle_{\text{random}}$, therefore the horizontal full line at 1 represents this value.

$\delta = 1$ because phylogenetically close species must have essentially the same number of contacts. Since for a greater phylogenetic distance there is also a greater diversity of species, $\Delta G(\delta)$ must also be an increasing function of δ . This may no longer hold for very large phylogenetic distances because of the scarcity of pairs of species in that situation.

Those two features are clearly displayed in the PERF system. Both disappear when the phylogenetic trees are randomized. The curves derived from the observed adjacency matrices of the NCOR, OLAU, ARR1 and ARR2 systems *without randomization* are compared in Fig.3 to an average of the null models for all systems obtained after 100 randomizations of each phylogenetic tree. They appear as random positive or negative fluctuations around the randomized average values thus not showing any appreciable trend making a difference between the observed and the randomized systems.

3.2. Generalized Attack Tolerance Curves

We assume that the system is attacked by eliminating the species of guild A in decreasing order of their degrees [17]. In each stage the GATC that we consider provides the average phylogenetic distance of the fraction of species of guild B that survive [18]. We have found that among a variety of other possibilities, this is the plot that more dramatically displays the subtle effects of phylogenetic proximity. The GATC starts at a value that corresponds to the average distance between the species of guild

B. Since successive stages of the attack produce average distances that are either the same or smaller, the GATC is supposed to decrease, reaching 0 when only one species of guild B is left.

If contacts were governed by phylogenetic proximity, close neighbors in the phylogenetic tree of guild A must have similar degrees. Assume that one starts by eliminating species belonging to one group of phylogenetically close generalists of guild A. Each elimination stage affects the group of specialists of guild B that are in turn assumed to be phylogenetic neighbors (see Fig.1). Successive extinctions of guild A produces little or no change in the average distance of survivors of guild B until the moment in which the last representative of the whole group of specialists of guild B becomes extinct. The average distance of the surviving species then drops significantly as a whole “branch” disappears from the tree. This fact leads to “plateaux” in the GATC, putting in evidence the existence of groups of phylogenetically close species of guild B successively disappearing as the elimination process of guild A progresses.

This GATC can be compared with a null model in which the tips of the corresponding phylogenetic trees are randomly sorted and many (100) realizations of the GATC’s are averaged. Upon randomizing any trace of phylogenetic proximity is eliminated but nestedness is nevertheless preserved. The GATC is therefore constantly equal to the average distance for guild B until the moment in which the last species is eliminated and only one species is left.

In Fig.4 we show several plots of the average distance between surviving species as a function of the number of elimination steps of their counterparts. In all cases the results of the null model are also drawn for comparison. The regular plateaux structure can clearly be observed in the benchmark PERF system. In the GATC for the NCOR system, traces of phylogenetic affinity can be observed both for plants and animals, leading to curves that fall well below those of the null model. The GATC for the OLAU system only displays some structure for plants. In the case of larger systems ARR1 or ARR2 there is no significant difference between the GATC’s of the real system and those of the null model.

An interesting consequence of this analysis is that the nested structure is not only robust face to attacks in which concern the preservation of the ecological system itself but also concerning the preser-

vation of its ecological diversity. In fact the PERF system loses its diversity as measured by the decrease of its average phylogenetic distances well before all real systems of comparable size.

3.3. A dynamic model

The influence of phylogenetic proximity can be cast into the form of a dynamic model of the kind explained previously by properly defining a CPR. There are two possible algorithms for an SNM fulfilling this. They involve the following steps.

A plant p is chosen at random and elements of the adjacency matrix K_{p,a_0} and K_{p,a_1} are also chosen at random such that $K_{p,a_0} = 0$ and $K_{p,a_1} = 1$. Next the following two sums are calculated:

$$S_0 = \sum_{p'} d(p, p') K_{p', a_0} \quad (6)$$

$$S_1 = \sum_{p'} d(p, p') K_{p', a_1} \quad (7)$$

A swap between this two elements i.e $K_{p,a_0}^{new} \rightarrow 1$ and $K_{p,a_1}^{new} \rightarrow 0$ is proposed and it will be accepted if, and only if, both animal species a_1 and a_0 do not become extinct due to the swapping.

Moreover, one of the two possible extreme CPR's defining the model is satisfied:

- **MIN:** the condition is $S_1 \geq S_0$
- **MAX:** the condition is $S_1 \leq S_0$

If either of the two conditions is not met, the proposed swapping is rejected. In order to proceed iteratively, all the above steps have to be repeated by interchanging in each step the role of plants and animals.

Within the MIN-CPR possibility, the animal counterpart that will finally be selected for p is such that all other plants p' that have some contact with it are *phylogenetically closer* to p . This is so because the sums S_0 and S_1 involve all phylogenetic distances between the plant p that has been selected at random and all other plants that make some contact with the two animals a_0 and a_1 . With this algorithm the configuration of contacts is progressively dominated by phylogenetic proximity: species of one guild are assumed to interact in the same fashion as the rest of species of the same guild belonging to their phylogenetic neighborhood.

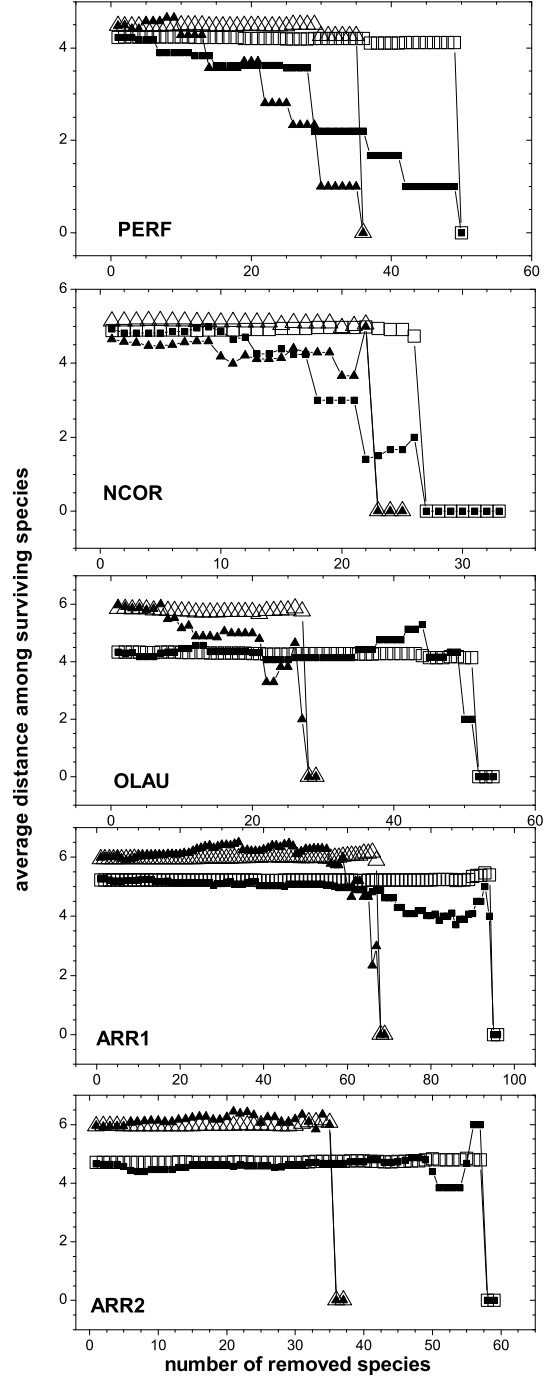


Figure 4: The average phylogenetic distance among surviving plants (animals) is plot as a function of the number of removed plant (animal) species of the other guild. Empty symbols correspond to the null model (100 random realizations of the phylogenetic tree), and filled symbols to the observed systems. Triangles (squares) correspond to plants (animals)

Within the MAX-CPR possibility, the animal counterpart that will be selected for the plant p is such that all other plants p' that have some contact with it are more *phylogenetically distant* to p . In this way the set of species that share contacts with p tends to have a greater phylogenetic diversity. In this alternative all species tend to be as generalist as possible as far their phylogenetic classifications are concerned. This alternative bears a greater similarity with the CPR considered in [6]. This is because a larger sum S_1 or S_0 is obtained not only by involving species that are more phylogenetically distant but also by involving a larger number of counterparts.

In order to check the ordering process generated by the SNM we define an effective distance between interacting species through:

$$D^{A,(P)} = \frac{1}{\langle d \rangle} \frac{\sum_{k,k'} d(k,k') \tilde{W}_{k,k'}}{\sum_{k,k'} \tilde{W}_{k,k'}} \quad (8)$$

In Eq.(8) $\tilde{W}_{k,k'}$ represents the unweighted adjacency matrix of the projected graphs for animals or plants. Its matrix elements are 1 (0) if two species share (do not share) mutualistic counterparts. This equation provides different results for plants or animals and should therefore be evaluated separately for the two guilds.

The sum in the denominator of Eq.(8) is just the number of terms appearing in the numerator, therefore D represents the average phylogenetic distance between species of the same guild that share at least one counterpart of the other guild. D is normalized by dividing it by the average phylogenetic distance $\langle d \rangle$ between *all* plant (animal) species of the system, namely

$$\langle d \rangle = \frac{\sum_{k,k'} d(k,k')}{N_{P,A}(N_{P,A} - 1)} \quad (9)$$

where $N_{P,A}$ is the number of plant or animal species of the system.

A value $D^{P,(A)} < 1$ indicates that phylogenetic proximity is a dominant effect, while $D^{P,(A)} \simeq 1$ is a signature that it is not relevant. We use its values to check for the convergence of the ordering process implied in the SNM.

In Figs.5 and 6 we plot the values of $D^{P,(A)}$ as a function of the number of iteration steps of the SNM for plants and animals for the two possible CPR's considered above. Concerning observed systems we only consider the NCOR system that

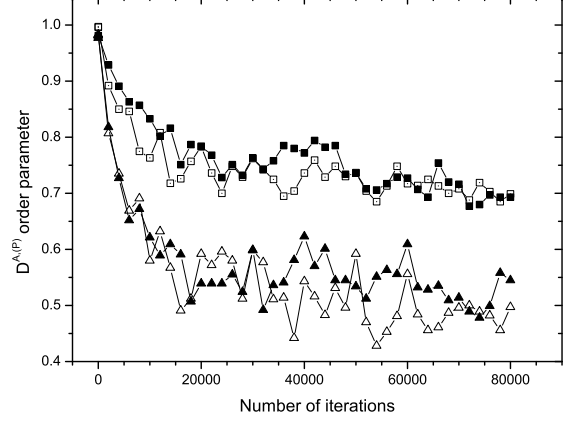


Figure 5: Order parameter of Eq.(8) $D^{P,A}$ as a function of the number of iteration steps of the SNM algorithm, using the MIN-CPR alternative. Filled symbols correspond to using as input to the SNM, the observed data of the NCOR system while empty symbols correspond to using as input, a random adjacency matrix with the same density of contacts as the one observed in nature. Triangles (squares) correspond to plants (animals).

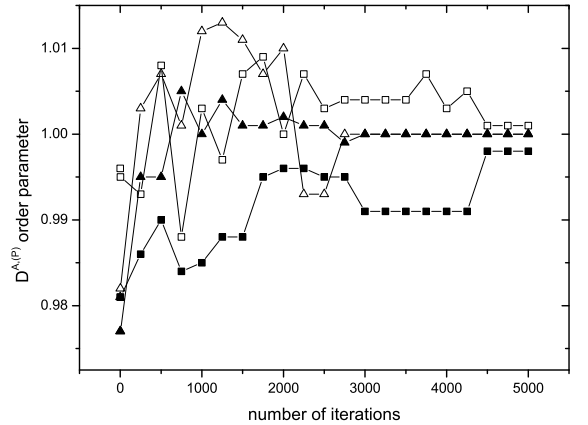


Figure 6: Value of the order parameter of Eq.(8) $D^{P,A}$ as a function of the number of iteration steps of the SNM algorithm using the MAX-CPR alternative. Notice that the vertical scale is strongly expanded as compared to that of Fig.5. Conventions are the same as in that figure.

is representative of a possible correlation between nestedness and phylogenetic proximity.

Two different initial conditions are plotted in each graph: one corresponds to the adjacency matrix has been reported from observation campaigns[4]. The other consists in an adjacency matrix of the same number of rows and columns and with the same number of contacts except for the fact that they are randomly distributed.

The initial values of $D^{P(A)}$ are very similar for both initial conditions. These are slightly below the average phylogenetic distances between species belonging to either of the two guilds. As the number of SNM iterations grows both CPR's produce values of $D^{P(A)}$ that reach asymptotic constant values that are essentially independent of the initial conditions, thus indicating that the system has achieved a stable and ordered pattern of contacts. However, while for the MIN-CPR case it is found that $D^{P(A)}$ stabilize at values that are significantly smaller than unity, for the MAX-CPR alternative it is found that they reach a stable value of 1.

The initial values of $D^{P(A)}$ indicate that species of the same guild sharing at least one mutualistic counterpart, are separated by an average distance that is very similar to the average distance of both phylogenetic trees. The fact that the observed value of $D^{P(A)}$ is close to the one obtained with a random matrix suggests that phylogenetic proximity may be regarded as an accidental situation involving few species of the system. While the MIN-CPR favors a contact pattern in which *both* guilds preserve their phylogenetic proximity, the MAX-CPR favors instead a more diversified situation in which species hold contacts with a phylogenetically diverse community.

The SNM algorithm can also be used to test if some given pattern of contacts is compatible with a CPR involving some kind of phylogenetic dependence. The asymptotic contact pattern can give a clue of what kind of pattern one should expect to find for each prevailing CPR. In Fig.7 we show the adjacency matrix of the SNM system as obtained after a great number of iterations of the SNM (panels (B) and (C)). These are the asymptotic contact patterns corresponding to the MIN-CPR alternative (panel B) and to the MAX-CPR alternative (panel C). In all cases the initial conditions are the empirically observed contact pattern (shown in Panel (A)). These matrices correspond to configurations in which $D^{P(A)}$ have reached an almost stationary value and are therefore nearly optimal in the sense

explained above. In the same figure the phylogenetic tree of plants and animals are shown to guide the eye.

The MIN-CPR corresponds to a rule in which the search of contacts is dominated by phylogenetic proximity. To better understand the emerging contact pattern (Panel (B)), one has to bear in mind that both animals and plants are considered on equal footing. This gives rise to an adjacency matrix that breaks in disconnected blocks in which phylogenetically close groups of one guild interact with similar groups of the other guild. This is the opposite of a nested scheme since upon a greater number of iterations of the SNM each species tends to specialize its contacts as much as possible. By the same token, generalists are ruled out of the system. The contact pattern of the NCOR system used as an initial condition, becomes therefore severely disturbed putting in evidence that it is unstable under the presence of the MIN-CPR in which phylogenetic proximity is the dominant rule.

A similar analysis for the MAX-CPR situation shows an opposite behavior. The SNM causes no drastic reorderings, reinforcing instead the presence of generalists and keeping the matrix mildly changed (see panel C). The observed adjacency matrix must therefore be considered stable under such CPR. This run of the SNM also provides additional information. The NCOR system hosts a group of animals that are phylogenetically close and that are all fairly good generalists (the *turdus* group). Such partial correlation between degree and phylogenetic proximity is not destroyed by the perturbations introduced by the SNM, if the prevailing CPR is of the MAX type (compare panels (A) and (C)).

An additional effect of the iteration of the MAX-CPR rule is that it leads to an asymptotically stable contact pattern that is almost perfectly nested. In panel (D) we show the adjacency matrices of panels (A) and (C) in which species have been reordered according to increasing degree, thus comparing the empirically observed nested structure of the NCOR system with an asymptotically nearly perfect nested pattern produced by the SNM using the MAX-CPR. Since the observed NCOR system is considerably nested, the effects of the SNM are not drastic.

The occurrence of phylogenetically close species with similar degrees and the occurrence of a nested

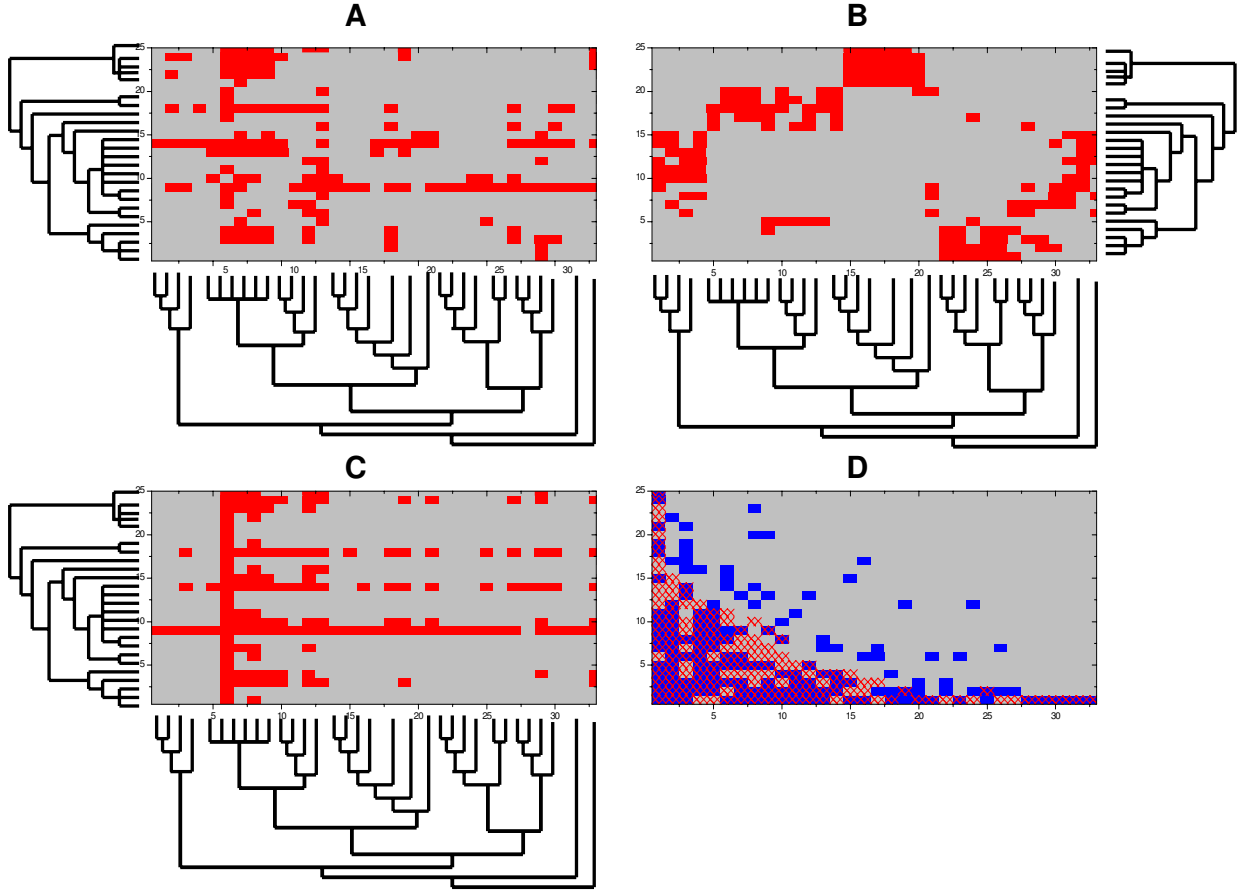


Figure 7: Several adjacency matrices of the NCOR system. Panel(A) the empirical contact pattern with species ordered according to the phylogenetic tree (shown along both margins of the matrix); panel(B): contact pattern produced by the SNM after 80,000 iterations using as input the empirical matrix shown in panel (A) and the MIN-CPR alternative, species in the same order as in panel (A); panel (C): contact pattern produced by the SNM after 5000 iterations, using MAX-CPR, species in the same order as in panel (A); panel (D) same contact pattern as panel (A) (dark pixels) and (C) (hatched pixels) but species are ordered by their degree. Dark pixels correspond to observed contacts (Panel (A)) while slanted pattern corresponds to the theoretical results (panel (C))

pattern should therefore be considered as independent from each other. When speaking of a *cause* for nestedness one should expect an element that is present in all the observed systems, with perhaps minor variations in few individual cases. We have found here that the only general cause of nestedness is essentially the same as the one reported in [6], i.e. a CPR that tends to place contacts on mutualist counterparts that already concentrate a large number of contacts. In the present framework nestedness emerges as a consequence of holding contacts with *phylogenetically diverse groups* of species. From this point of view, phylogenetic proximity has therefore to be considered as *compatible* with a rule inducing nestedness but is far from being a cause of it.

4. Conclusions

We have tried several tests to gauge the influence of phylogenetic proximity in the occurrence of nestedness. They were performed on several real systems whose adjacency matrices are reported in the literature (NCOR, OLAU, ARR1 and ARR2 in Ref.[4]) and also on PERF, a benchmark of an ideal system in which degrees and phylogenetic proximity have been tailored to display a very strong correlation.

In these tests we have considered the ecological similarity between species, the dispersion in the degrees of species as a function of the phylogenetic distances separating them and the shape of the generalized attack tolerance curves (GATC). In all cases we have also compared the results obtained from real or ideal systems with those of null models constructed by randomly sorting the tips of the phylogenetic trees.

The dependence of the ecological similarity or the dispersion of the degrees with the phylogenetic distance have proven to be essentially undistinguishable from the one obtained for the randomized systems in all cases considered. The ideal, perfectly organized system shows regular trends of both parameters as a function of the phylogenetic distance that are not met by real systems. One must however bear in mind that both tests are somewhat “coarse grained”, in the sense that they involve the adjacency matrix as a whole.

To circumvent this problem we define a GATC in which we plot the average distance between the fraction of species of one guild that survive after increasing fractions of the counterpart guild are elim-

inated. The effect of phylogenetic proximity reveals itself as the occurrence of plateaux in an otherwise monotonously decreasing function. The results indicate that the influence of phylogenetic proximity is more an accident than a rule. It can only be detected in the NCOR system while in the rest (OLAU, ARR1 and ARR2) only traces can sometime be observed. Moreover the results indicate that the nested structure of the network makes the system robust in terms of ecological diversity. In fact, considering the average phylogenetic distance as a measure of the ecological diversity, real systems preserve this better than the PERF system.

In order to investigate for possible causes of nestedness rooted in phylogenetic proximity we have complemented the static tests mentioned above with the use of the SNM. An example of the outcome of this test is reported focusing only in the NCOR system.

The general conclusion that stems from the dynamic tests is that an interaction between species that exclusively prefers phylogenetic proximity can never give rise to a nested contact pattern. A nested contact pattern turns out to be unstable in the presence of such interaction rule. A way to see this is by realizing that such interaction mechanism relies in the generalized occurrence of species that are specialists therefore ruling out generalists. However, these are an indispensable ingredient of a nested organization. A contact rule governed by phylogenetic proximity for *both mutualists guilds* therefore tends to destroy a nested pattern of contacts. These tests indicate in addition that the adjacency matrices would tend to break down into separate, nearly independent components in which groups of phylogenetically close neighbors of both guilds hold contacts among each other but not with the rest of the species of the ecological system. The stability analysis performed using the SNM proves that a contact pattern such as the ideal PERF system is unstable under the perturbations produced by a contact rule favoring phylogenetic proximity.

We have also proved that an alternative interaction pattern dominated by *phylogenetic diversity* is instead a much better approach to describe real situations. This interaction mechanism is one in which species are assumed to hold contacts with counterparts that are already visited by a greater *diversity* of species. This could be interpreted as a stylized version of a rule by which all species tend to put the least possible requirements in their feeding or pollinizing counterparts. It is worth to stress

that this rule is fully consistent with the ones tested in Refs.[6] and [2] and provides an additional proof of the validity of the possible sources of nestedness mentioned there. In those situations highly realistic degree distribution functions and contact patterns are produced by the SNM by only assuming that species tend to hold contacts with species that already hold a greater number of contacts.

The second contact rule by which one species tends to visit a set of counterparts having a maximal diversity agrees in fact with one of the two schemes suggested in the opening figure of Ref.[4]. In addition if a group of phylogenetically close species happen to have similar contact patterns, the corresponding contact pattern turns out to be stable under such maximal diversity interaction rule. A set of phylogenetically close species of the NCOR system that also are good generalists is stable under the perturbations of the SNM. This points in the direction that, although phylogenetic affinity can not determine the existence of nestedness it is fully *compatible* with it.

The results obtained with the dynamic tests are consistent with those obtained with the static ones. Both point into the same direction of considering the correlation of phylogenetic proximity and degree, if any, is largely accidental and that it can never be considered as a general cause of nestedness. A dominant cause of the generalized nestedness found in mutualistic ecosystems perhaps lies on the simple fact that species that we observe in real systems today are those that tend to put the least possible restrictions on their mutualist counterparts.

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- [17] This is the only order that allows to see some structure in the ATC of nested systems. In the limit of perfect nestedness, an attack in increasing order only shows its effect when the last species is eliminated.
- [18] As a complement, one can also consider the fraction of species of guild B that become extinct (*secondary extinctions*) because they are left without a mutualistic counterpart in guild A.